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Bayesian Criterion Update with Working Memory Explains the Trial-to-trial Variability of Perceptual Decision and Cortical Representation of Decision Uncertainty

베이시언 추론과 작동 기억에 기반한 지각 판단 기준 갱신 모델: 인간 행동과 뇌영상의 시행간 변이에 대한 연구

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Abstract

We change our perspective to the world depending on moment by moment influx of the new information. Because our references of the world are updated every moment, we used to decide on something as a different one under the different context, although the object is same. The aim of this study is to investigate this variable characteristic of human mind. Our question is that why and how reference of the world is restlessly adjusted? By implementing ring-size discrimination task, we reproduced the phenomenon, in which the decision reference of subject was not static but modulated by previous stimulus, in controlled experimental condition. Also, to investigate the phenomenon in model-based approach, we developed the model of trial-to-trial update of decision criterion by using Bayesian inference and generated 3 simpler versions of the model. By applying all the 4 models to behavior and fMRI data and comparing their predictions, we found that decision criterion is not only modulated by sequence of previous stimuli but also anchored by long-term criterion in trial-to-trial manner and also that the modulation was well captured in Bayesian framework. In this regards, we suggest that dynamic nature of world reference is the consequence of human nature in searching for most probable understanding of the reference combining long-term and recent information.

Keyword : perceptual decision-making, decision criterion, Bayesian inference, fMRI, trial-to-trial variability, decision uncertainty
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Introduction

One of the postulates of the special theory of relativity reveals the lack of an absolute reference frame (Einstein 1905). Einstein discarded the absolute state of rest and developed a theory of relative space and time. His theory has been successful in describing our world. From this perspective, we can ask ourselves whether there is such thing as an absolute reference when judging the size of an object. Typically, we judge something large or small without an explicit reference. For example, we may describe a bathtub "long", when its length is 10 m. On the other hand, a measure of "10 m" can be described short when it is about a swimming pool. This example illustrates that our decision on the same object can vary depending on the context. For another example, imagine that we lived for a whole year in a mansion with a 10m-long bathtub. Then our prior standard for the typical length of bathtubs is likely to increase. The latter example shows that our prior criterion can adapt to our recent experience of external stimuli—the likelihood distribution. Put together, these examples imply that there are no such perceptual entities that are absolutely small or large. We simply cannot decide whether something is small or large depending only on sensory information itself but can only judge whether something is smaller or larger than a pre-defined, and adaptable, decision reference. In this regard, perceptual decision is relativistic by nature.

A number of studies have reported that subject decides by using relative information of stimulus (Garner 1954; Baird et al. 1980; Vlaev et al., 2011; Sharif et al. 2016). Although these works clarified that relativistic information should be considered for describing decision, it is unclear that why subjects made decision relying on relativistic information. Some researchers proposed and tested computational models to describing sequential dependence, in which subjects manipulated relativistic feature of current to previous information (Stewart et al., 2002; Lages & Treisman 2010; Frund et al., 2014). However, models were remained heuristics so that it was

hard to understand why subjects manipulated relative information of current stimulus. Therefore, there have been tries to develop normative model to understand sequential dependency in respect to Bayesian theorem (Raviv et al. 2012; Norton et al. 2017). The advantage of this approach would be that success of it can suggest that subject' s sequential dependence can be also described as optimal behavior, in which prior information is combined with current information to give statistically optimal decision (Ernst & Banks 2002; Kording & Wolpert 2004). However, because heuristic and non-normative models performed better than normative model in the researches, it was remained unclear that subject' s relativistic behavior is comprehensible or not in respect to normative sense.

Here we start from clarifying definition of criterion for investigating relativistic feature in human subject. We propose that decision criterion is center of stimulus measurements (COS). The primary advantage of the idea is that it unifies previous stimulus and prior criterion information into a single physical variable (i.e. COS). Therefore, previous stimulus information and long-lasting criterion information acquire role of likelihood and prior of current criterion respectively allowing us to develop normative criterion update model. To investigate validity of normative criterion update model, we also developed 3 alternatives including heuristic working memory model, which was best model on the other researches (Raviv et al. 2012; Norton et al. 2017), and compared each other in several aspects encompassing goodness-of-fit, correlation between current choice and previous stimulus, trial-by-trial variability of L-choice proportion, covariance between response time and predicted uncertainty, and trial-by-trial prediction of fMRI BOLD signal. By doing this, we found that the normative criterion update model performed better than the others. Therefore, we propose that relativistic decision-making behavior can be understood in terms of normative sense.

Method

Observers

Among total 41 paid volunteers, 18 individuals (9 females; 20-30 years old) participated in the main fMRI experiment and 23 the others (11 females; 18-36 years) only performed behavioral experiment without fMRI scanning. The data of later group was published previously (Choe et al. 2014, Choe et al. 2016) and the subjects in fMRI experiment were those whom participated in another experiment (Choe et al. 2014), in which subjects followed same procedures, but data was re-collected for whole brain fMRI analysis and it was not published before. All of the observers were normal or corrected-to-normal vision and participated with informed consent in accordance with the guidelines and approval of the Institutional Review Board at Seoul National University. All observers were naive to the purpose of the study.

Experimental setup

Experimental setup was detailed in Choe et al. 2014 and Choe et al. 2016. We also introduce the procedure, but please refer the papers for more information.

fMRI experiment. 3 Tesla Siemens Tim Trio scanner equipped with a 12-channel Head Matrix coil at the Seoul National University Brain Imaging Center was used for collecting MR data. Stimuli were generated using MGL (http://justingardner.net/mgl) and MATLAB (MathWorks) on a Macintosh computer. To view stimuli, observers looked through an angled mirror attached to the head coil. LCD projector (Cannon WEED SX60) onto a back-projection screen was used to produce stimulus and the projector was located at the end of the magnet bore with a viewing distance of 87cm yielding a field of view of 22X17 ° .

Behavior only experiment. For behavior data (23 of 41 participant) out of fMRI scanner, stimulus was presented on a gamma-linearized 22-inch CRT monitor (Totoku CV921X CRT monitor) operating at vertical refresh rate of 180Hz and a partial resolution of 800X600 pixels, while subjects performed in a dimly lit room. Monitor was located at a distance of 90 츠 from the observer. The observers sat on a height-adjustable chair. And, their head was supported by a forehead and chin rest (HeadSpot, UHCOTech), which were together with the monitor, mounted on a height-adjustable table. EyeLink 1000 Desktop Mount (SR Research) was used to collect ocular information. The eye data was not shown hear and published elsewhere (Choe et al. 2016).

Behavioral protocol

Behavior protocol was also detailed in Choe et al. 2014 and Choe et al. 2016, because the data we used here are same with theirs. Please refer the papers for more information

fMRI experiment. On onset of trials, the observer briefly viewed a small fixation dot (diameter, 0.12 ° ;0 luminance, 321 cd/m^2) at the center of a dart (luminance, 38 cd/m^2) screen. The observer was forewarned by a small but visible increase in the size of the fixation dot (0.12 ° to 0.18 °) in diameter of an upcoming presentation of the test stimulus. That test stimulus consisted of the brief (300 ms) presentation of a thin (full-width at half-maximum of a Gaussian envelope, 0.17 °), white (321 cd/m^2), dashed (radial frequency, 32 cycles/360 °) ring that counter-phase-flickered at 10 Hz. At the same time with onset of stimulus, observers were allowed to report the ring's size ("small" or "large") using a left-hand or right-hand key respectively, guessing if necessary. Observers were instructed to maintain strict fixation on the central dot, unless they would be unable to detect the change in the fixation dot signaling a forthcoming brief target stimulus and, thus, their performance would be hampered.

Observers performed 54 practice trials and then 180 threshold-estimation trials before the main experimental scan runs, inside the scanner but without being scanned. Threshold-estimation trials were performed with intertrial interval of 2.7 s. On the trials, one of 20 different-sized rings was presented and the sequence was adjusted following a multiple random staircase procedure (four randomly interleaved 1-up-2-down staircases, two starting from the easiest stimulus and the other two starting from the hardest one) with trial-to-trial feedback. The psychometric curves were fitted by a Weibull function with maximum likelihood approach. From the fitted Weibull function, the size contrast (*SC*) associated with 70.7% correct was estimated. And the SC was used to determine the radii (r_M, r_S, and r_L) of the three ring stimuli (S, Small; L, large; M, medium) used in the main scan runs: $r_M = 2.84°$; $r_S = (1 + SC)*r_M$; $r_L = (1 + SC)*r_M$. In the main experimental scan runs, observers performed 208 trials in total, while being scanned over eight, 343.2 s functional scan runs. Stimulus, three different-sized rings, were presented in the order defined by an m-sequence (base 3, power 3; nine S- and L-rings and eight M-rings were presented; all scan runs started with two M-rings) (Buracas and Boynton, 2002) to null the autocorrelation between stimuli. Intertrial interval was 13.2 s (Fig. 1*A*, trial structure). Each observer practiced on the task intensively (6000 trials with short, 2.7 s, inter-trial interval over 6 sessions) outside the scanner, before participating in the fMRI experiments. Observers also performed retinotopy-mapping before the ring size discrimination task.

Behavior only experiment. All observers participated in a total of three daily sessions: one for practice (315 short-interval trials), one for threshold SC estimation (315 short-interval trials plus four runs of the main task, 108 trials), and the other for six runs of the ring-size discrimination trials with eye position being monitored (162 trials). The stimuli and procedure were same with those of the main fMRI experiment except for the followings. First, absolute luminance values of stimulus were changed to 30 cd/m^2 and 3 cd/m^2,

respectively, although the luminance contrast between the stimuli and the background remained comparable with that in the fMRI experiment. Second, larger number of trials was used for determining the threshold SC value (315 instead of 180). Third, one more M-ring trial was added to a given run. Fourth, 156 trials were given in total over six, 342.2s runs. Lastly, the number of practice trials was smaller than that of the fMRI experiment. Lastly, at the beginning of each session, a visually guided saccade task taking ~4min was conducted.

Main postulations of models.

Main postulations were specified. The other assumptions were also clarified in following descriptions.

P1. Primary postulation in the models is that subjects discriminated size of stimulus by comparing trial-to-trial measurement of stimulus (m_{stm}) with that of decision criterion (m_{cri}). For example, we postulate that subject would determine size of given ring as large (D_l and D_s denote large- and small- decision respectively), if m_{stm} was larger than m_{cri}. Therefore, if m_{stm} and m_{cri} were sampled from stimulus population defined by $N(m_{stm}|\mu_{stm}, \sigma_{stm})$ and $N(m_{cri}|\mu_{cri}, \sigma_{cri})$, then probability of large choice $p(D_l)$ would be area under receiver operation characteristic (ROC) curve:

$$p(D_l) = \Phi\left\{\frac{\mu_{stm}-\mu_{cri}}{\sqrt{\sigma_{stm}^2+\sigma_{cri}^2}}\right\} \quad \text{(Eq.1)}$$

, where Φ is standard normal cumulative distribution (Marzban 2004).

P2. The second postulation is that m_{stm} and m_{cri} were sampled from static normal distributions of m_{stm} (i.e. sampled from 3 different populations for each ring in mean but sharing same standard deviation σ_{stm}) and changeable normal distribution of m_{cri}. Because stimuli were controlled to be physically identical by experimenter, it is not too hard to say that m_{stm} populations are

static across task. On the other hands, because not only external factor like stimulus but also internal factor like working memory can affect internal state of subjects (i.e. decision criterion) and experimenter cannot control it, we cannot say that m_{cri} population stays on its initial state across task. Therefore, it would be more reasonable to allow those internal factors to have a degree of freedom. In this sense, we allowed it to be updated trial−by−trial to capture flexibility of the internal factors.

P3. The working memory capacity was characterized by leak ratio r. The third postulation was developed for providing with rationale that experience of previous trials can affects decision of current trial through working memory. Specifically, if stimulus measurement of ith trial back were $m_{st(i)}$, then resultant stimulus measurement (m_{rs}), remained in working memory on current trial, is weighted average of the previous trials' measurements:

$$m_{rs} = \frac{\frac{1}{r}m_{stm(1)}+\frac{1}{r^2}\cdot m_{stm(2)}+\cdots+\frac{1}{r^n}\cdot m_{stm(n)}}{\frac{1}{r}+\frac{1}{r^2}+\cdots+\frac{1}{r^n}} = \frac{\sum_{i=1}^{n}\frac{1}{r^i}\cdot m_{stm(i)}}{\sum_{i=1}^{n}\frac{1}{r^i}}.$$

Because stimulus measurement of ith trial back is randomly sampled from population of previous stimulus, we cannot determine definite value of resultant stimulus on current trial but its distribution. If measurements are sampled from different but normally distributed populations, we know their weighted average is also normal distribution and can analytically derive its mean and standard deviation as

$$\mu_{rs} = \sum_{i=1}^{n}\beta_i \cdot \mu_{stm(i)} \text{ and } \sigma_{rs}^2 = \sum_{i=1}^{n}\beta_i^2 \cdot \sigma_{stm}^2 \quad \text{(Eq.2)}$$

, where β_i is weight of ith trial back stimulus measurement defined as

$$\beta_i = \frac{\frac{1}{r^i}}{\sum_{i-1}^{n}\frac{1}{r^i}}.$$

Note that $\sigma_{stm(i)} = \sigma_{stm}$, because we assumed stimulus measurement were sampled from populations sharing same standard deviation (P2).

P4. The fourth postulation is that decision criterion is inferred center of stimulus measurements (COS). Specifically, optimal criterion in 2 alternatives forced choices task (2AFC) would be center of stimulus space as long as given stimulus measurement is distributed symmetrically on stimulus space. So, we can deduce that single trial' s stimulus input is not only stimulus evidence but also evidence of decision criterion, because stimulus input is current evidence for COS.

$$\theta_{stm} = \theta_{COS} = \theta_{cri}$$

Therefore, if we introduce prior distribution of COS, then decision criterion will be updated from its prior to posterior by being multiplied by likelihood (i.e. current stimulus). We will specify the details of criterion update mechanism in next model specification section.

Model specification

What is only difference between models is rule and ingredient for updating decision criterion, because we did not adopt trial-by-trial systematic variability in m_{stm}. Therefore, each model is characterized by its unique population for sampling m_{cri}. Here is specification of how each model formed and updated population of m_{cri} population. See table 1 for summary of the specification.

Static criterion model (SC). SC assumes m_{cri} is randomly sampled from long-term criterion (LTC) normal distribution: $N(m_{cri}|\mu_{LTC}, \sigma_{LTC})$. In other words, SC did not update its decision criterion trial-by-trial. Therefore, its decision outcome would have no systematic variability, if stimulus was held to be same. In short. m_{cri} was randomly sampled from normal distribution defined as:

$$\mu_{cri} = \mu_{LTC} \text{ and } \sigma_{cri} = \sigma_{LTC}$$

Non-Bayesian criterion update with full working memory model (NBFW). NBFW uses nothing but history of stimuli in developing decision criterion. NBFW assumes that population of m_{cri}

is distribution of weighted average of previous m_{stm}. NBFW adopts working memory capacity by leak ratio r. Thus, if ith back m_{stm} population is normal distribution, in which mean and standard deviation are $\mu_{stm(i)}$ and $\sigma_{stm(i)}$ respectively and leak ratio is r, then mean and standard deviation of population of m_{cri} would be

$$\mu_{cri} = \sum_{i=1}^{n} \beta_i \cdot \mu_{stm(i)} \text{ and } \sigma_{cri}^2 = \sum_{i=1}^{n} \beta_i^2 \cdot \sigma_{stm}^2, \text{ where } \beta_i = \frac{\frac{1}{r^i}}{\sum_{i=1}^{n} \frac{1}{r^i}}.$$

Note that we did not consider effect of previous stimulus over 9 trials back (~120 sec, $n = 9$).

Bayesian criterion update with limited working memory model (BLW). BLW takes two sources for decision reference: previous stimulus and long-term criterion. However, its working memory could not extend more than 1 previous trial so that it has "limited" in its name. Trial-by-trial criterion measurement of BLW is a value maximizing product of inferred distributions of COS, $df(\theta_{COS})$, which are calculated from 1 trial back stimulus measurement $m_{stm(1)}$ and measurement of LTC, m_{LTC} as following.

$$\left[\frac{df(\theta_{COS})}{d\theta_{COS}}\right]_{\theta_{COS}=m'_{cri}} = 0$$

$$f(\theta_{COS}) = p(\theta_{COS}|m'_{stm(1)}, m'_{LTC})$$

$$= \left[p(\theta_{COS}|m_{stm(1)}) \cdot p(m_{stm(1)})\right] \cdot \left[p(\theta_{COS}|m_{LTC}) \cdot p(m_{LTC})\right]$$

$\propto p(\theta_{COS}|m_{stm(1)}) \cdot p(\theta_{COS}|m_{LTC})$, if $p(m_{stm(i)})$ and $p(m_{LTC})$ are uniform distribution

$\propto p(\theta_{stm(1)}|m_{stm(1)}) \cdot p(\theta_{LTC}|m_{LTC})$, if $\theta_{COS} = \theta_{stm} = \theta_{LTC}$, see P4

$\propto p(m_{stm(1)}|\theta_{stm(1)}) \cdot p(m_{LTC}|\theta_{LTC})$, if $p(\theta_{stm(i)})$ and $p(\theta_{LTC})$ are uniform distribution

$\propto \frac{1}{\sqrt{2\pi\sigma_{stm}^2}} e^{\frac{-(m_{stm(1)}-\theta_{COS})^2}{2\sigma_{stm}^2}} \cdot \frac{1}{\sqrt{2\pi\sigma_{LTC}^2}} e^{\frac{-(m_{LTC}-\theta_{COS})^2}{2\sigma_{LTC}^2}}$, for P2 and assumption of SC

$\propto N(\theta_{COS}|\mu_{COS}, \sigma_{COS})$

, where $\mu_{COS} = \frac{\sigma_{stm}^2 m_{LTC} + \sigma_{LTC}^2 m_{stm}}{\sigma_{stm}^2 + \sigma_{LTC}^2}$ and $\sigma_{COS} = \frac{\sigma_{stm}^2 \sigma_{LTC}^2}{\sigma_{stm}^2 + \sigma_{LTC}^2}$

therefore, $m_{cri} = \frac{\sigma_{stm}^2 m_{LTC} + \sigma_{LTC}^2 m_{stm}}{\sigma_{stm}^2 + \sigma_{LTC}^2}$ (Eq.3)

Eq.3 indicates that inferred measurement of criterion m_{cri} is weighted sum of m_{LTC} and $m_{stm(1)}$.

$$m_{cri} = \beta_{LTC} m_{LTC} + \beta_{stm(1)} m_{stm(1)}, \text{ where } \beta_{LTC} = \frac{\sigma_{stm}^2}{\sigma_{stm}^2 + \sigma_{LTC}^2},\ \beta_{stm} = \frac{\sigma_{LTC}^2}{\sigma_{stm}^2 + \sigma_{LTC}^2}.$$

When latent variable (LV) is weighted average of variables (Var) randomly sample from normal distribution, population of the latent variable also follows normal distribution with mean and standard deviation as following.

$$\mu_{LV} = \sum_{i=1}^{n} \beta_i \cdot \mu_{Var(i)} \text{ and } \sigma_{LV}^2 = \sum_{i=1}^{n} \beta_i^2 \cdot \sigma_{Var(i)}^2$$

Therefore, population of m_{cri} is $N(m_{cri}|\mu_{cri}, \sigma_{cri})$, where $\mu_{cri} = \beta_{LTC} \cdot 0 + \beta_{stm(1)} \cdot \mu_{stm(1)}$ and $\sigma_{cri}^2 = \beta_{LTC}^2 \cdot \sigma_{LTC}^2 + \beta_{stm(1)}^2 \cdot \sigma_{stm}^2$ and $\beta_{LTC} = \frac{\sigma_{stm}^2}{\sigma_{stm}^2 + \sigma_{LTC}^2}$, $\beta_{stm(1)} = \frac{\sigma_{LTC}^2}{\sigma_{stm}^2 + \sigma_{LTC}^2}$. If we do not implement bias is LTC population (i.e. $\mu_{LTC} = 0$). Then, we can analytically calculate $p(D_l)$ by using Eq.1.

Bayesian criterion update with full working memory model (BFW). BFW is same with BLW except its working memory capacity spans more than 1 trial back. Therefore, we would substitute $m_{stm(1)}$ for measurement of resultant stimulus m_{rs} in BLW as follows.

$$\left[\frac{df(\theta_{COS})}{d\theta_{COS}}\right]_{\theta_{COS}=m_{cri}} = 0, \text{ where } f(\theta_{COS}) = p(\theta_{COS}|m_{rs}, m_{LTC})$$

If we refer to **Eq.2** for distribution of m_{rs} and assume that $p(m_{rs})$, $p(m_{LTC})$, $p(\theta_{stm(i)})$ and $p(\theta_{LTC})$ are uniform, $\theta_{COS} = \theta_{stm} = \theta_{LTC}$ and no bias on LTC, then distribution of m_{cri} would be $N(m_{cri}|\mu_{cri}, \sigma_{cri})$, where $\mu_{cri} = \beta_{rs} \cdot \mu_{rs}$, $\sigma_{cri}^2 = \beta_{LTC}^2 \cdot \sigma_{LTC}^2 + \beta_{rs}^2 \cdot \sigma_{rs}^2$, $\beta_{LTC} = \frac{\sigma_{rs}^2}{\sigma_{rs}^2 + \sigma_{LTC}^2}$, $\beta_{rs} = \frac{\sigma_{LTC}^2}{\sigma_{rs}^2 + \sigma_{LTC}^2}$. Therefore, $p(D_l)$ can be calculated by using Eq.1.

Model fitting

Once population of m_{cri} was specified trial-by-trial, then trial-by-trial likelihood of choice L can be calculated by using Eq.1.

Each model was fitted individually to search for parameters set ($\vec{\theta}$) of given model to maximize sum of each trial' s log−likelihood (LL) of choice as follows

$$
\begin{aligned}
LL(\vec{\theta}; model) &= logp\left\{data|\vec{\theta}; model\right\} \\
&= log\prod_{t=1}^{N} p\left\{\hat{C}_t|s_t, h_t, \vec{\theta}\right\} \\
&= \sum_{t=1}^{t} logp\left\{\hat{C}_t|s_t, h_t, \vec{\theta}\right\}
\end{aligned}
$$

,where $\vec{\theta}$ is set of fitting parameters, $\hat{C}_t$, s_t and h_t are observed choice, stimulus and stimulus history on tth trial and N is the number of trials of a single subject (Qamar et al. 2013). $\vec{\theta}$ of each model is specified on Table1.

We used fminsearbnd.m (John D' Errico, MathWorks) searching for global maxima of log likelihood and separated fitting stage into three level for initial parameter randomizing. In the first stage, we randomly sampled 1000 combination of initial parameters and performed a maximum of 50 line searches for each. Ranges of initial values are fixed and uniformly distributed from 0 to 100 for all parameters, but there was no bound on the fitted values. And then, we selected best 50 initial parameter combinations from first stage, started fitting in the 50 initial points with a maximum of 100,000 lines (Qamar et al. 2013). Lastly, when fitting converged on parameters set, we restarted for another maximum of 100,000 lines at the converged parameters for each of 50 initial points. By doing this, the fitted parameter set showing maximum log likelihood was selected.

Note that we assumed that working memory could not extend across runs and its capacity is constrained 9 trials at most (~120 second) within runs. Thus, first 8 trials of each run could not use full working memory capacity for developing decision criterion. Instead, they had to form decision criterion with previous but within run

stimuli. We also assumed that choices of first trials of each run are generated with purely random fashion.

Model (abbrev., color)	Fitting parameters	mean of criterion measurements	std. of criterion measurements	beta specification
Static criterion model (SC)	σ_{stm} σ_{LTC}	$\mu_{cri} = \mu_{LTC}$	$\sigma_{cri} = \sigma_{LTC}$	
Non-Bayesian full working-memory model (NBFW)	σ_{stm} r	$\mu_{cri} = \sum_{i=1}^{n} \beta_i \cdot \mu_{stm(i)}$	$\sigma_{cri}^2 = \sum_{i=1}^{n} \beta_i^2 \cdot \sigma_{stm}^2$	$\beta_i = \frac{\frac{1}{r^i}}{\sum_{i=1}^{n} \frac{1}{r^i}}$
Bayesian limited working-memory model (BLW)	σ_{stm} σ_{LTC}	$\mu_{cri} = \beta_{stm(1)} \cdot \mu_{stm(1)}$	$\sigma_{cri}^2 = \beta_{LTC}^2 \cdot \sigma_{LTC}^2 + \beta_{stm(1)}^2 \cdot \sigma_{stm}^2$	$\beta_{LTC} = \frac{\sigma_{stm}^2}{\sigma_{stm}^2 + \sigma_{LTC}^2}$ $\beta_{stm(1)} = \frac{\sigma_{LTC}^2}{\sigma_{stm}^2 + \sigma_{LTC}^2}$
Bayesian full working-memory model (BFW)	σ_{stm} σ_{LTC} r	$\mu_{cri} = \beta_{rs} \cdot \mu_{rs}$	$\sigma_{cri}^2 = \beta_{LTC}^2 \cdot \sigma_{LTC}^2 + \beta_{rs}^2 \cdot \sigma_{rs}^2$	$\beta_{LTC} = \frac{\sigma_{rs}^2}{\sigma_{rs}^2 + \sigma_{LTC}^2}$ $\beta_{rs} = \frac{\sigma_{LTC}^2}{\sigma_{rs}^2 + \sigma_{LTC}^2}$ $\mu_{rs} = \sum_{i=1}^{n} \beta_i \cdot \mu_{stm(i)}$ $\sigma_{rs}^2 = \sum_{i=1}^{n} \beta_i^2 \cdot \sigma_{stm}^2$

Table 1. Fitting parameters, mean and standard deviation of criterion measurement population for each model. β_i for BFW is same with that of NBFW.

Model comparison

Information criterion and likelihood ratio test. To compare goodness-of-fit, we implemented information criterions and likelihood ratio test (LRT). Because SC is not nested model of the others, it was compared by using Akaike information criterion (AIC) and Bayesian information criterion (BIC) with BFW. On the other hands, NBFW and BLW are simpler form of BFW. Specifically, if σ_{LTC} is larger enough than σ_{stm}, we can see that β_{LTC} is to be 0 and β_{rs} is to be 1 so that BFW is reduced to NBFW (Table 1). Also, if r is large enough, then $\beta_i = 1$ for $i = 1$ and $\beta_i = 0$ otherwise, which will result in BFW becomes BLW. The nested property was also demonstrated by fitting parameters (Fig. 2B, C). Therefore, model comparison between BFW, BLW and NBFW could be implemented by using likelihood ratio test.

Prediction of L choice proportion. Models predict probability of L choice trial-by-trial according to Eq1. To compare prediction and observation, it is required to divide whole trials into a few bins, because what we are able know from observation of single trial is not probability but binary decision variable, while model predicts proportion of choice for each trial. It makes possible to calculate proportion of L choice from each of bin and compare it with averaged value of predicted proportion of L choice on the corresponded trials. Each bin has same number of trials as long as whole trials can be divided into same number of bins. If not, all bins other than one bin

have same number of trials minimizing difference between the number of trials between bins.

However, analysis using bin cannot help confronting with problem of how should deal trials having same value. Because SC cannot update criterion, its predictions of proportion of D_L are constrained only to stimulus to predict same proportion of D_L for each stimulus respectively. Likewise, although BLW updates criterion, because the only source to update criterion are 3 stimuli of 1 back trial, its maximum number of predictions of L choice limited to 9 from combining 3 pre−stimuli and 3 current−stimuli. Moreover, although NBFW and BFW can generate a number of different predictions trial−by−trial, some subjects were well described by few proportions of D_L in the case that choice of the subjects showed large correlation between stimulus and their choice meanwhile dependence on previous experience was negligible.

All of this could generate artifact when bins are composed of the same number of trials, because trials predicted to show same proportion of D_L would belong to different bins. For example, when there is a set of alphabets $\{a_1, a_2, a_3, b_4\}$ while subscription denotes implicit character (e.g. observation sequence), if we divide then into $\{a_1, a_2\}$, $\{a_3, b_4\}$ and there was significant difference between them, we cannot say that the difference resulted from effect of alphabet, because there could be an implicit character: observation sequence. To resolve the problem, we adopted bootstrap approach. First, trial order was randomized and sorted as proportions of D_L. Then, trials were divided into bins and proportion of D_L was calculated on each bin by using observed data and models' prediction. Lastly, we repeated above steps 10000 times and took mean values of D_L proportions as the valid values. Those steps were applied to subjects who are predicted to use less than 21 proportions of D_L. Unless, bootstrap was neglected for boosting up analysis.

Effect of previous stimuli. To measure effect of previous stimuli, we used part correlation coefficient as currency, in which correlation was calculated between current choices and stimulus of

ith trial back when effect of current stimulus was linearly regressed out only from previous stimulus. To secure trials as many as possible, we did not choose multiple regression for describing correlation between sequence of previous stimulus and current choice. To be specific, because we assumed that sequential effect does not extend over run−to−run, we should exclude a number of initial trials of each run from analysis to estimate sequence of previous stimulus from current choice maintaining the number of trial sequence. Although part−correlation controlling only current choice also has disadvantage in that autocorrelation of stimulus could disturb result, we presented stimulus in the order defined by m−sequence (Buracas and Boynton, 2002) to null the autocorrelation between stimuli.

To determine which model could capture effect of previous stimulus, simulation was preformed 100,000 times for each trials and each subject. For a single iteration, choice of all trials was predicted by sampling m_{cri} and m_{stm} from their predicted populations and comparing them. And then, part−correlation between the simulated choice and stimulus of ith trial back was calculated under control of current stimulus. Lastly, averaged value across trials of the part−correlation coefficients was obtained on individual manner.

Correlation between response time and decision certainty. There have been a number of researches reporting positive correlation between response time (RT) and decision certainty (Kiani et al. 2014). Although RT is not ideal proxy of uncertainty, RT has positive correlation unless task difficulty is not too hard (Binder et al. 2002). To quantify certainty, we implemented with $p(D_l)$, which is the ratio of large choice under given condition. We assumed that certainty over D_l is monotonically increase with D_l and for D_s vice versa. Moreover, we also assumed that mental scale is not linear to D_l or D_s but logarithm following ideas of Weber and Fechner (Dahaene 2003). Therefore, we defined decision uncertainty of t trial (U_t) as follows.

$$U_t = log\{1.5 - max[p(D_{l(t)}), p(D_{s(t)})]\}$$

We, then, investigated which model' s uncertainty is best for predicting RT by using general mixed linear model by using RT as response variable, uncertainty as fixed effect and individual difference as random effect.

MRI data acquisition and preprocessing

MRI data acquisition specification was also described in Choe et al. 2014. We also summarized the detail here.

For each observer' s brain, two 3D, T1-weighted, high-resolution ($1 \times 1 \times 1mm$) anatomical scans were acquired with an optimized protocol (MPRAGE; field of view (FOV), $256mm$; repetition time (TR), 1.9 s; time for inversion, 700 ms; time to echo (TE), 2.36 ms; flip angle (FA), 9°), averaged to improved image fidelity.

T2*-weighted functional images were obtained with a gradient EPI pulse sequence for the main experimental scans. The parameters for main experimental scans were as follows: TR, 2.2s; TE, 30 ms, FA, 73° ; FOV, 208mm; slice thickness, 3mm; slices 32 oblique transverse slices; bandwidth 790 Hz/Px; effective voxel size $3.3 \times 3.3 \times 3.0mm$. At the beginning of each functional session, a high-resolution ($1.08 \times 1.08 \times 3.3mm$) T1-weighted inplane image was acquired with the same slice prescription as the functional images for the image-based registration.

All functional EPI images were motion-corrected and coregistered to the high-resolution reference anatomical volume of the same observer' s brain via the high-resolution inplane image (Nestares and Heeger, 2000). After coregistration, spikes in fMRI signal was eliminated by using despike function in AFNI. And then, slice timing was corrected to be middle of acquisition sequence for each TR. The corrected images were normalized to be resampled to $3 \times 3 \times 3mm^3$ sized voxels and spatially smoothed with $8 \times 8 \times 8mm^3$ FWHM Gaussian smoothing kernel. We used SPM8 (http://www.fil.ion.ucl.ac.uk/spm) (Friston et al., 1996; Jenkinson et al., 2002) for motion-correction and coregistration, SPM12 for slice

timing correction, normalization and smoothing and AFNI for de-spiking.

The individual voxels' time-series were linearly detrended, high-pass filtered by 5th order butterworts filter with 132s cut-off frequency, divided by their means to convert them from arbitrary intensity units to percentage modulations (Smith et al. 1999) using custom scripts in MATLAB (MathWorks). Lastly, to regress out noise, we randomly sampled time series of 3000 voxels from CFS, averaged them and orthogonalized time series of each voxel in cortex to the averaged CFS signal using recursive Gram-Schmidt orthogonalization algorithm (spm_orth.m function in SPM12). The first 6 (of 208; a length of a trial; 13.2s) frames of each scan were discarded to minimize the effect of transient magnetic saturation and allow the hemodynamic response to reach steady state.

fMRI data analysis

Our aim in fMRI signal was to search for neural signature of criterion update. To meet the purpose, we concentrated on confirming that BOLD signals correlated with decision uncertainty were modulated not only across stimulus size but also across criterion size within same stimulus. To find neural signal reflecting decision uncertainty, we implemented TR-wise general mixed linear model by using fitglme.m function (MathWorks).

We did not implement GLM approach, which has been widely adopted by fMRI researchers by convolving canonical hemodynamic response function for the following reasons. 1) We could not have reasonable assumption for BOLD gain modulated by latent variable (i.e. decision uncertainty). For example, although model predicts uncertainty was modulated by 120%, BOLD signal correlated with uncertainty could vary 101%, 110%, 130% or 200%. However, if we search for neural correlate by adopting GLM with regressor convoluted by canonical hemodynamic response function (hfr), we cannot help assuming gain of BOLD signal modulated by regressor. 2) There can be a dissociation between time of peak of BOLD signal

and most informative time correlated with latent variable. Although the discrepancy could be generated by difference in event duration and the problem would be resolved if we design regressor reflecting the difference in duration, it is also impossible to deduce how much event duration gets different according to magnitude of latent variable, if the event could not be controlled by experimenter. Therefore, if we design regressor with identical event duration for uncertainty and convolve with hrf, the most informative time point would be peak of BOLD signal. 3) Although canonical hrf is used widely by fMRI investigators, hrf is different voxel-to-voxel and individual-to-individual. Therefore, if there is a way to investigating BOLD signal without canonical hrf, it would be better way. 4) To resolve difference in statistical precision between estimations of regressor coefficient, we did not take multi-level analysis (i.e. 1st level, GLM for individual subject; 2nd level, t-test for testing significance of GLM coefficient across subjects), in which significances of coefficient of individual subjects were assumed to be same. In fact, if we implemented multi-level approach and if there was an outlier showing unusually large coefficient value with poor statistical precision, 2nd-level inference would reach to incorrect conclusion to show high significance, because we assume identical statistical power of the coefficients across subjects.

To address problems mentioned above, we implemented TR-wise general mixed linear model. It tests group-level significance of linear covariance between BOLD amplitude and latent variable for each time points and each voxel. The details of the procedure is specified as following. 1) We standardized latent variables for each individual by using z-score to match variance of latent variables while BOLD signals were remained to percent signal, 2) gathered BOLD signal sharing same time point in respect to stimulus onset so that we have vectors of latent variables and BOLD signal in one-to-one manner for each time point and each voxel, and 3) implemented general mixed linear model designed to have both fixed effect of decision uncertainty and intercept and have mixed effect of individual subject for both decision uncertainty and intercept.

Then, we have statistical parametric map for each TR. To perform ROI analysis, we defined voxel cluster as ROI, if it met all the following criterions: 1) contiguous voxels more than 11 voxels ($> 297mm^3$) within a single time point, 2) each voxel shows p−value < 0.001, 3) on one of the time points within −15.4 to 24.2s from stimulus onset spanning from −6TR to 12TR or, in other words, from onset of previous to end of next trials.

Result

Task design and model description

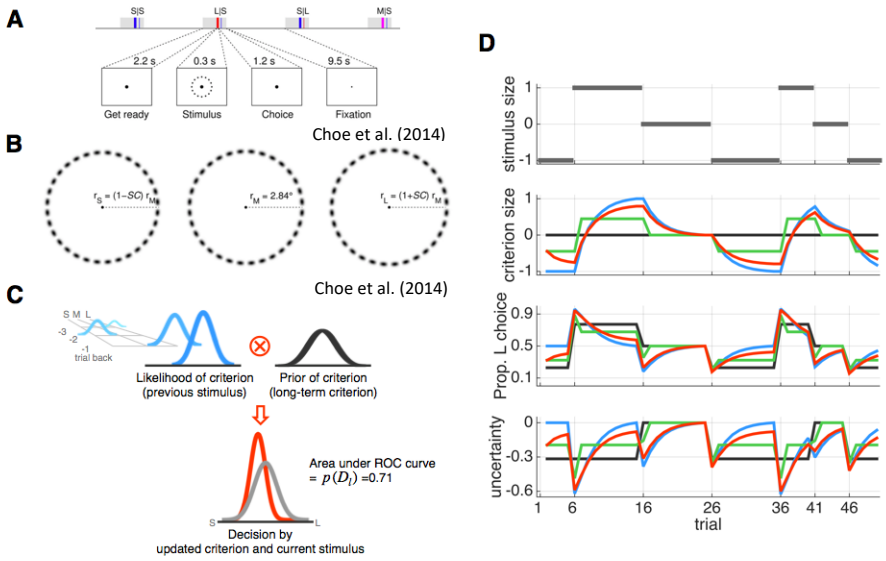

Figure 1. Task design and model description. ***A,*** Four exemplar trials are shown. A trial (13.2s) is composed of pre-cue (2.2s), stimulus (0.3s), choice (1.2s) and fixation waiting next trial (9.5s). Letters above gray bar and colors of vertical line indicate stimulus and choice on given trial. ***B,*** Example of three different sized rings. Eccentricities of small and large rings are deviated by size contrast (SC) from that of medium ring. The luminance polarity is reversed hear for illustrative purpose. ***C,*** Criterion update and decision rule of BFW. Upper row describes criterion update and the lower specifies decision rule. Blue, black, red and gray lines describe previous stimuli, long-term criterion, updated criterion and current stimulus respectively. ***D,*** Model behaviors for example stimulus sequence. Gray line describes stimulus sequence. Black, blue, green and red indicate predictions of SC, NBFW, BLW and BFW respectively.

Subjects performed ring-size discrimination task (Fig. 1A, B). Because subjects did not know existence of M-ring and SC was adjusted for each subject to give comparable difficulty between subjects (Fig. 1B, see Method), subjects had to perform task under a lot of uncertainty.

To investigate decision-making mechanism, we build 4 different models called static criterion model (SC), non-Bayesian full working memory model (NBFW), Bayesian limited working memory model (BLW) and Bayesian full working memory model (BFW). As an example, operation of BFW was illustrated (Fig. 1C). Primary proposition for criterion update is that measurement of decision criterion is nothing but center of stimulus measurement (COS, see Method), if stimulus measurements were symmetrically distributed

and 2 alternatives were forced. In this respect, we could realize that trial-to-trial input of stimulus has to be ingredient for criterion update, because it is another evidence of COS. In other words, stimulus is not only used for generating current trial' s decision (i.e. gray curve) but also for updating decision criterion for next trials as a likelihood of decision criterion (i.e. blue curve). By assuming prior distribution of criterion measurement (i.e. black curve), we could derive trial-to-trial variability of criterion measurement population (i.e. orange curve). Then, probability for making L-choice $p(D_l)$ was calculated with trial-by-trial manner by using receiver operating characteristic (ROC) analysis (Eq. 1). Specification of models were summarized by table (Table 1).

To explicitly demonstrate distinctions between models, we manipulated example stimulus sequence and applied models to the stimulus (Fig. 1D). First of all, criterion size of SC is constant to result in variability of $p(D_l)$ modulated only by current stimulus. Therefore, uncertainty was larger on M-ring trials and smaller on S-, L-ring trials. However, the other models adopt previous stimulus to update decision criterion. For example, NBFW develops criterion by depending only on previous stimulus. Therefore, its criterion position converges to stimulus, if same stimulus had been given for a number of consecutive trials like from 6 to 16, from 16 to 26 and from 26 to 36 trials. As a result, $p(D_l)$ also converges to 0.5 and uncertainty is maximized for the stimulus sequence, because distributions of criterion and stimulus become indistinguishable. On the other hands, BLW implements both previous stimulus and LTC for developing criterion, while it cannot utilize 2 back trial and more previous stimulus information. Therefore, its criterion size is updated but has no monotonic increase or decrease. Lastly, BFW combines LTC and full sequence of previous stimulus. Therefore, because LTC anchors decision criterion to center of decision space, its criterion does not converge to stimulus like NBFW, even if a number of same stimulus had been shown. But, it still has monotonic increase/decrease as to stimulus sequence, since population of

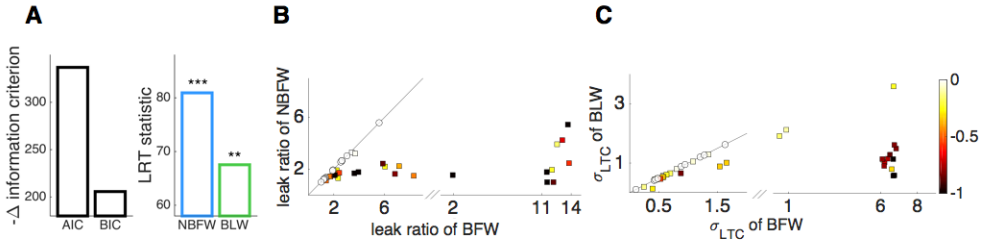

Figure 2. Fitting results. ***A,*** Difference of information criterions between SC and BFW (left). Test statistics of likelihood ratio test (LRT) between BFW and the nested models of BFW: NBFW and BLW (right). Asterisks indicates p-value **<0.01, ***<0.001. ***B, C,*** Each circle represents each subject. Scale of x-axis is changed to log10 on the right side of a couple of inclined lines. Gray line is diagonal. Scale of face colors are same with color bar on the right. ***B,*** Fitting parameter comparison between BFW and NBFW. Face colors of markers indicate difference of log10-likelihood between NBFW and BFW (NBFW-BFW). For the subjects having standard deviation of LTC of BFW was larger than 10, marker was described as circle. Square describes the others. ***C,*** Fitting parameter comparison between BFW and BLW. Colors of circles show difference of log10-likelihood between BLW and BFW (BLW-BFW). For the subjects having leak ratio of BFW was larger than 10, marker was described as circle. Square describes the others.

resultant stimulus got being sharpened as same stimulus evidences were accumulated.

Fitting results and goodness-of-fit

Before investigating details of model's predictions, we firstly compared their goodness of fit by using information criterion and LRT. Firstly, because SC is not nested by any other, we implemented Akaike information criterion (AIC) and Bayesian information criterion (BIC) and compared them with those of BFW (Fig. 2A left). Because fitting performance of SC was much poorer than BFW, we could infer that decision of subjects were affected by previous stimulus rather than independent of previous trial.

Also, because we could confirm that NBFW and BLW are nested by BFW (Fig. 2B, C and Table 1), model comparison between NBFW, BLW and BFW was executed by LRT. Specifically, if σ_{LTC} is larger enough than σ_{stm}, β_{LTC} and β_{rs} become 0 and 1 respectively making $\mu_{cri} = \mu_{rs}$ and $\sigma_{cri}^2 = \sigma_{rs}^2$ (Table 1). So, BFW collapses to NBFW. In other words, because observers cannot acquire enough criterion information from LTC, if σ_{LTC} is too large, they should have relied largely on working memory to build criterion. And, it made σ_{LTC} of BFW useless and, thus, goodness-of-fits of NBFW and BFW same (Fig. 2B, circle). In fact, subjects predicted as having large σ_{LTC} by BFW, depicted as circle, showed identical leak ratio to that of NBFW implying that BFW is reduced to NBFW. Furthermore, we also confirmed that BFW predicted better as leak ratio fitted by BFW is departed from that of NBFW.

On the other hands, in comparing BFW with NBFW, if leak ratio of BFW is large enough to make β_i is 1 if $i = 1$ and 0 otherwise, μ_{rs} and σ_{rs} become $\mu_{stm(1)}$ and $\sigma_{stm(1)}$ respectively (Table 1). It means that BFW becomes BLW, if leak ratio is large enough. In other words, if leak ratio has large value, then effect of previous stimuli more than 1 trial back in updating criterion is weakened resulting that criterion update is governed only by stimulus of immediately preceding trial and LTC, which is the rationale of BLW. In fact, fitting parameters showed that when leak ratio is larger, σ_{LTC} of BFW converges into that of BLW and likelihoods of BLW and BFW in predicting behavior become identical (Fig 2C, circles). It reveals that BLW approximates BFW, when subjects manipulated most previous stimulus and LTC for developing criterion. However, BFW showed better performance than BLW as σ_{LTC} increase.

In this regards, we confirmed that NBFW and BLW are nested models of BFW and proceeded to LRT to compare their goodness of fit (Fig 2A right). LRT revealed that BFW was better than NBFW and BLW. As a results, goodness-of-fit analysis provide us with an evidence that BFW is comprehensive model encompassing individual variability in long-term criterion and working memory capacity.

BFW was better than the other models in predicting trial-by-trial variability of proportion of L choice

To make sure how decision was modulated by previous stimulus, we assorted trials by their stimulus history (Fig. 3). Being compared with prediction of SC, observation showed systematic variability within fixed stimulus (Fig. 3A). Therefore, it looks that SC had a problem in its assumption. Specifically, data showed consistent positive linear trend of $p(D_l)$ within a fixed current stimulus as previous stimulus changes from L-rings to S-rings trials. The positive linear trend implies that decision reference was attracted by previous stimulus to make opposite decision more on later trials.

However, although it is clear that subjects used previous stimulus for current choice, there could be a few of different ways in

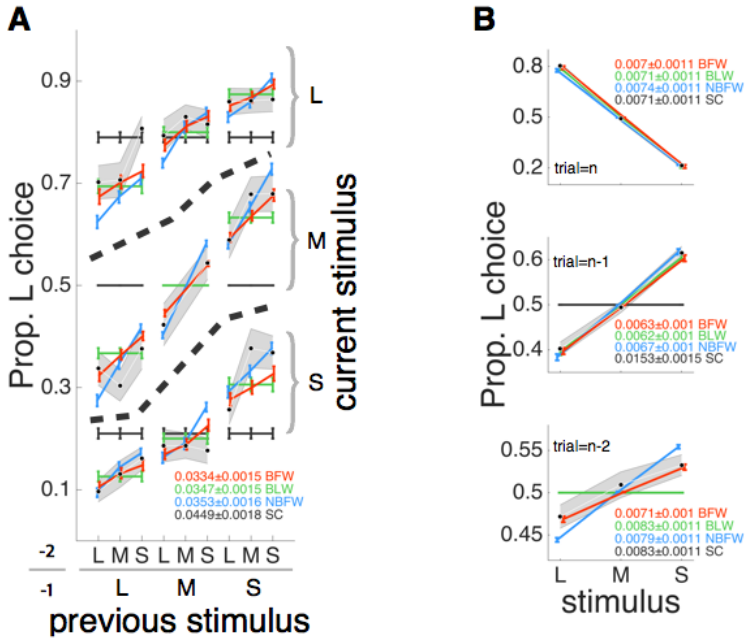

Figure 3. proportion of large choice given current and previous stimuli. ***A, B,*** Observed data points are showed as black circle and shaded error bar. Predictions of models are specified by colored error bar. SC, NBFW, BLW, BFW are described by dark, blue, green and red respectively. Error bar is standard error of mean (SEM) across all 41 subjects and numbers are averaged mean squared error (MSE) of individual subject with its SEM across subjects. X-values were intentionally and slightly deviated model-to-model for illustrating purpose, although they share same category. ***A,*** Dashed bold lines separate trials by current stimulus: current L-ring trials are above the upper line, M-ring and S-ring trials are middle of dashed lines and below of lower dashed line respectively. X-axis informs stimulus of 1 and 2 previous trials. ***B,*** Y-values were calculated from current trial's choice (i.e. trial=n). But, time points of stimuli for binning trials were different for each subplot. Time points used for brining are current (n), most previous (i.e. n-1), and 2 trial back (i.e. n-2) for top, medium, and bottom subplot respectively.

manipulating previous stimulus for current trial' s decision. For example, it is possible that LTC was updated by immediately preceding trial' s stimulus, that subjects developed criterion just depending on previous stimulus information, or that combination of previous stimulus sequence and LTC information could form decision criterion. Each of instance is correspond to BLW, NBWF and BFW respectively (Fig. 3A). First of all, it was revealed that BLW has a systematic error, when trials were sorted by 2 back stimulus. Specifically, BLW could not capture variability of $p(D_l)$ on fixed -1 trial' s stimuli. The failure of BLW was obvious, if all trials were sorted by 2 trial back stimuli (Fig 3B, bottom). Also, although prediction of NBFW looks capture general trend (Fig. 3A), it also has biased prediction when trials were sorted by 2 back stimulus (Fig.

3B, bottom). Specifically, it predicts $p(D_l)$ larger and smaller than observation when given 2-back stimulus was small and large respectively. However, BFW not only showed smallest prediction error of the models but also did not have biased prediction.

Therefore, by investigating prediction of $p(D_l)$, we can also conclude that subjects cannot be described by either only working-memory or LTC update using most previous stimulus but can be understood better, if we assume that they used not only full-working memory but also long-established criterion information for performing the task.

BFW was better than the other models in predicting correlation between current choice and previous stimulus

To concentrate on effect of previous stimulus to current choice, we analyzed part-correlation between current choice and stimulus of nth back trial with regress out current stimulus from previous stimulus to rule out the case that correlation between previous stimulus and current stimulus could lead to correlation between previous stimulus and current choice as by-product. Data showed negative correlation existed not only on immediate preceding trial but also on more previous ones (Fig. 4).

However, SC did not have any correlation between current choice and previous stimulus, because its decision was completely made by stochastic process of current stimulus and static criterion.

Moreover, although overall MSE of BLW are rather comparable to that of BFW, it completely failed in predicting correlation on 2 trial lag, which is result from nature of BLW that it did not consider effect of 2 and more back trials. We also can deduce that observed correlation on 2 and 3 trial lags are not by-product of 1 trial lag, because BLW succeeded in 1 trial lag but failed on 2 and 3 trial lags. To be specific, it is possible that 2 back trial's stimulus has correlation with current choice although it has no causality to updating decision criterion, if it was correlated with 1 back trial's

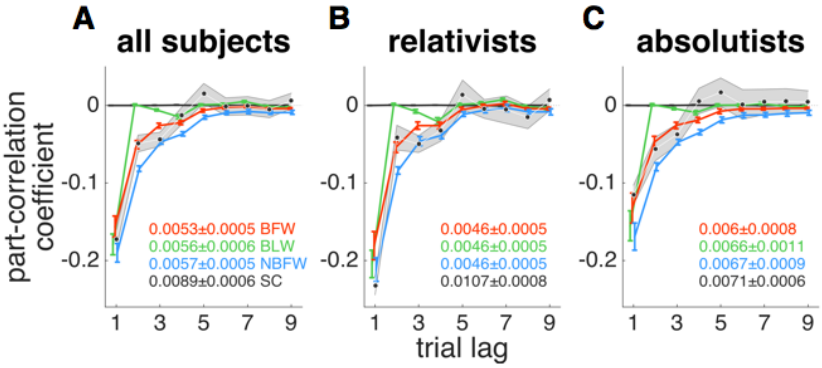

Figure 4. Effect of previous stimulus to current choice. Correlation between current choice and previous stimulus with control of current stimulus to previous stimulus is y-values. Dark circles and gray shade lines are data point and its SEM. Colored error bars represent each model. Numbers are averaged MSE and its SEM across subjects. Error bar is SEM of each point across subjects. ***A,*** Data describes all 41 subjects. ***B, C,*** Subjects were divided into two sub-groups by their part correlation coefficient of 1trial lag. ***B,*** 20 subjects showing more negative coefficient are called relativists. ***C,*** The other 21 subjects were characterized as absolutist.

stimulus and the stimulus of 1 trial lag affected decision criterion. Therefore, failure of BLW on 2, 3 trial lag indicates that there is unique covariance between current choice and stimulus on 2, 3 trial lag. Otherwise, BLW could also showed correlation on 2, 3 trial lag, because it caught covariance between current choice and stimulus on 1 trial back. Therefore, working memory extending over 1 trial range was engaged in subjects' decision making.

As to NBFW, although it looks unclear that NBFW has systematic error on all subject plot (Fig. 4A), it is obvious that NBFW has biased error in predicting absolutists (Fig. 4C), in which NBFW has larger correlation between current choice and previous stimulus than observation. The reason is as following. Absolutist is half of subjects who showed smaller impact of 1 back stimulus to current choice. In other words, decision criterion of absolutists was less attracted by previous stimulus so that absolutists made decision more likely to be absolute size of stimulus than the other subjects group called relativists (Fig 4B). For example, if two S−ring were given consequently, ideal absolutists would decide current choice as S, because their criterion is negligibly drawn to previous stimulus. But, ideal relativist would be confused, because decision criterion would be attracted to S−ring by 1 trial back stimulus to make it hard to distinguish criterion from current S−ring stimulus measurement population. In this regards, to characterize absolutists, NBFW has no

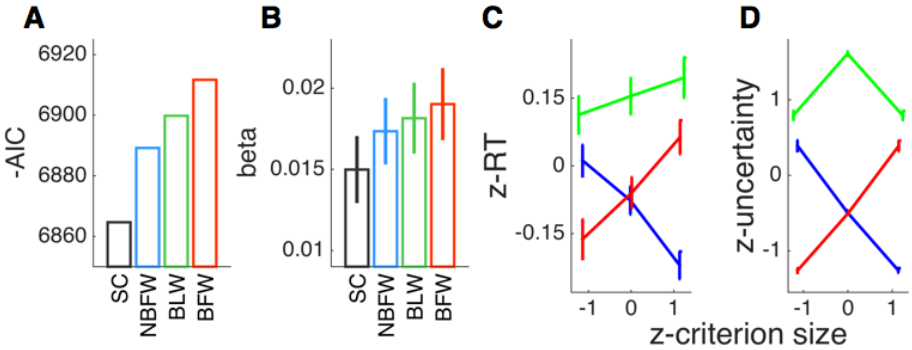

Figure 5. RT and Uncertainty. ***A,*** AICs predicting RT with uncertainty by using general linear mixed effect model. ***B,*** Fixed effect coefficient of general linear mixed effect model. Error bar is its standard error. ***C, D,*** Red, green, and blue are trials of current L-, M-, S-ring respectively. Trials are binned into 3 equal-trial bins by their criterion size within fixed stimulus. X-value of each bin is averaged criterion size across subjects. Error bar is standard error of mean across subjects. Uncertainty and criterion size were predicted by BFW. ***C,*** Variance of RT with fixed stimulus and varying criterion size. ***D,*** Uncertainty variation as to criterion size.

choice but to increase working memory capacity to engage stimulus information as much as possible to reduce effect of each stimulus. It is why NBFW has more long-tailed correlation between current choice and previous stimulus. However, observation tells that absolutists are more likely to be described as whom developed sharp LTC population rather than have strong working memory capacity in that BFW was fitted to be comparable correlation tail length to relativists.

Therefore, part-correlation analysis also revealed that subjects cannot but be described by combination of full working memory and long-term criterion factor.

BFW was better than the other models in predicting trial-by-trial variability of uncertainty

Although RT is not perfect substitute for decision uncertainty, RT has been widely used as a variable closely related to uncertainty (Kiani et al., 2014; Binder et al., 2002). In this regards, we investigated whether variance of RT under fixed stimulus has correlation with decision uncertainty or not. As being expected, RT had positive linear relationship with uncertainty (Fig 5B). Interestingly, the covariance between RT and uncertainty was strongest when uncertainty was derived by BFW (Fig 5A).

Thus, we used uncertainty calculated by BFW to test correlation between uncertainty and RT under fixed stimulus (Fig 5C, D). If RT is ideal proxy of uncertainty, it would have "X hat" feature (Fig 5D), which is prediction of BFW. For example, under given S-ring (i.e. blue line), uncertainty would increase as criterion size is closer to S-ring. In fact, we can confirm that blue line ascends as criterion size decrease. Also, if M-ring (i.e. green line) is presented, uncertainty would be highest when criterion size was identical with M-ring size and decrease as criterion diverges from medium size to make inverted V shape.

When we assorted RT by using current stimulus and criterion size, we could find that RT reveals "X bar" feature (Fig 5C). When we implemented 2 way ANOVA with repetition, we could confirm that it had significant interaction $F(2,2,4)=9.78$, $p<10^{-6}$ and row effect $F(2,2,4)=37.76$, $p<10^{-14}$. Therefore, we can conclude that RT was also modulated by decision criterion update on S- and L-ring trials and showed overall increase for M-ring trials but did not showed covariance with uncertainty within M-ring trials.

Neural activity was described better by criterion update model than static criterion model

We also investigated whether signature of criterion update exists in neural activity. First of all, we compared neural correlates of uncertainty calculated by BFW with that by SC, because uncertainty of SC cannot incorporate criterion update but include variance of stimulus. Therefore, if there was no criterion update, uncertainty might be modulated only by stimulus and, thus, SC could perform well in searching for neural correlate of uncertainty. However, if there was substance of criterion update, SC would fail in finding uncertainty signal whereas BFW did not. In this regards, our prediction was that nodes of attention network would be more recruited by the more plausible model in describing decision-making mechanism. And, as we expected, uncertainty regressor of BFW

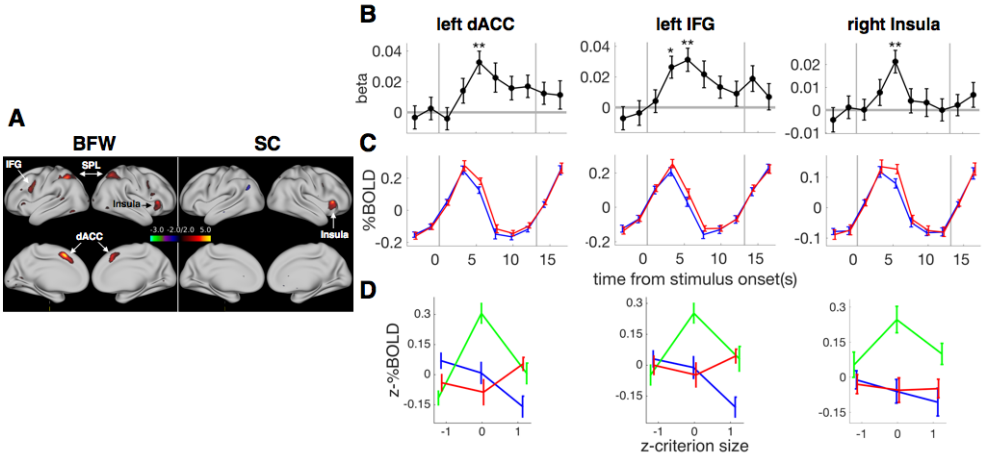

Figure 6. Neural signature of criterion update. ***A,*** Brain areas showing correlated activity with uncertainty predicted by either BFW (left) or SC (right) on 3rd time point after stimulus onset. Color scale indicates log10 of p-value obtained by GLME. Sign of color bar indicates sign of fixed effect coefficient. All voxels showing lower p-value than 0.01 were rendered. ***B, C, D,*** ROI analysis correlated with uncertainty predicted by BFW (dACC and IFG) or SC (insula). Left and right gray vertical lines represent current trial's and next trial's stimulus onsets. ***B,*** Beta is fixed effect coefficient of GLME with its SEM on error bar. Asterisks represent uncorrected p-value range *<0.01, **<0.0001. Beta in dACC and IFG was calculated by uncertainty obtained by BFW whereas beta in insula was acquired by uncertainty predicted by SC. ***C,*** Red and blue lines are averaged BOLD signal across subjects with higher and lower 50 percentile trials of uncertainty respectively. But, red line illustrates M-ring trials while blue shows L- and S-ring trials in insula. Error bar is SEM across subjects. ***D,*** Trials were sorted into 3 bins in proportion within fixed stimulus by using criterion size predicted by BFW. Blue, green and red lines show S-, M-, and L-ring trials respectively. %BOLD signal on 3rd time point after stimulus onset was used in all ROIs. Error bar is SEM across subjects.

could engage attention network nodes like ACC, SPL, IFG and insula (Fig. 6A left). On the other hands, SC showed poor performance in finding ROIs relevant to uncertainty (Fig. 6A right). Therefore, we could confirm that neural activity was also described better by criterion update than static criterion paradigm.

We, then, proceed to ROI analysis (Fig. 6B, C, D). Under threshold of p−value < 0.0001 and 10 contiguous voxels within single time point for defining ROI, we searched for clusters satisfying the criterion from 7 previous to 11 later time points (i.e. 18 time points) to stimulus onset covering all the time point of previous, current and later trials and could identify that left dACC and left IFG met the criterion by using uncertainty of BFW and right insula could satisfy it under uncertainty of SC on 3rd time point after stimulus onset (Fig 6B). Also, we could find that gain of BOLD activity has region−to−region inhomogeneity. In other words, linear coefficient was not consistent across ROIs (Fig6. B). And, all the ROIs showed discrepancy between peak and most informative timing (Fig6. B, C). Finally, by using two−way ANOVA with repetition, we found that dACC and IFG have significant row effects, dACC: $F(2,2,4)=3.86$, $p<0.05$; IFG: $F(2,2,4)=6.35$, $p<0.01$, and interaction, dACC: $F(2,2,4)=12.78$, $p<10^{-8}$; IFG: $F(2,2,4)=7.08$, $p<10^{-4}$. Therefore, it

was confirmed that activity of dACC and IFG was modulated by combined effect of criterion and stimulus. However, right insula did not showed significant interaction, $F(2,2,4)=2$, $p=0.10$, but showed strong row effect, $F(2,2,4)=14.18$, $p<10^{-5}$. Nevertheless, its activity also modulated by criterion size as predicted by BFW on M-ring trials.

Thus, we have a conclusion that effective and substantial uncertainty variable implemented by brain cannot be originated solely from external stimulus input but is product of interaction between stimulus and criterion.

Discussion

Based on the premise that a decision criterion is an estimate of the center of stimuli experienced previously, we developed a Bayesian inferene model that forms and updates the decision criterion by combining the prior belief and the recent sensory experiences on a trial-to-trial basis. The key probability distributions of our model were defined as follows: (i) the prior was modeled as the distribution of stimulus measurements maintained for a long-term period; (ii) the likelihood refers to the distribution of weighted averages of stimulus measurements in previous trials; (iii) the posterior is the normatively inferred distribution of decision criterion sizes. With these representations and computations of probability distributions, our model readily accounted for the trial-to-trial variability of response times, choices and the influences of previous stimuli, significantly better than the alternative models with non-Bayesian inference or limited working memory. Furthermore, the decision uncertainty estimated by our model well explained the neural activities in the cortical regions that are previously known as representing decision uncertainty, to a degree substantially higher than what can be explained by the model that assumed the static criterion.

Trial-to-trial update of decision criterion under Bayesian inference

If we just consider current stimulus as only causal factor for choice while all the other factors were considered as noise like SC, we would be ignorant of how previous history affected current perceptual decision-making. And, it is the way majority of perceptual studies were investigated (Frund et al., 2014). However, what failure of SC in capturing behavior in a few aspects told us is that decision of subjects was systematically affected by previous stimulus. Furthermore, NBFW, a model designed to capture sequential

dependence of choice on previous stimulus (Norton et al., 2017) , was also not successful in that its prediction for absolutists, whose choice were less affected by previous stimulus and well explained by current stimulus than the others called relativists, was systematically different from observation implying that there was another factor other than current and previous stimulus. Specifically, NBFW describes absolutist as who had strong working memory capacity in developing decision criterion resulting in that it was hardly swayed by individual stimulus to be stable across session, while there was prolonged tail of correlation between current choice and previous stimulus. However, span of the correlation was shorter than prediction of NBFW. It implies that there is another component in developing decision criterion other than working memory. In this regards, by postulating that optimal decision criterion is center of stimulus measurement, we could develop criterion update models using Bayesian inference: BLW and BFW. In other words, mechanism for inferring optimal position of decision criterion was suggested with 2 variations. BLW used only immediately preceding stimulus as likelihood of decision criterion whereas BFW covers previous stimulus up to 9 trial back. The imprecise prediction of BLW makes us confirm that influence of previous stimulus was fetched over interval of single trial to affect decision criterion. On the whole, because both BFW successfully predicted a few facets of observation than the others, we summarize result as subjects' relativistic behavior on perceptual decision-making were most well described by Bayesian decision criterion update models so that we propose that relativistic behavior can be normative.

dACC and SPL were engaged in uncertainty rather than updating internal representation

Because model predicts both internal representation of decision criterion and uncertainty, we could investigate that whether activity of dACC and SPL co-fluctuated with either criterion update cost (O' Reilly et al. 2013) or uncertainty (Shenhav et al. 2014). Our

task and model have advantage in resolving the problem, because updating cost and uncertainty is negatively correlated. To be specific, model predicts criterion update cost would be increased as size of criterion and that of current trial' s stimulus show larger difference. However, decision uncertainty would decrease as size difference between stimulus and criterion is widened. In this respects, because activity of dACC and SPL was correlated with uncertainty, our data supports activity of dACC and SPL were not correlated with updating cost but uncertainty.

Criterion as the center of stimulus measurement

Our primary assumption for conceptualizing model is that criterion is nothing but center of stimulus measurement. The assumption makes it possible that stimulus is not only used for being compared with criterion but also for updating criterion. Although there were studies using criterion for describing decision-making (Lages & Treisman 2010), they lacked what is meaning of criterion and why the criterion is updated. We believe that the nature of criterion can be widened further than perceptual decision-making to non-perceptual studies like economics.

Limitation of BFW and future direction

Although BFW could describe well decision-making using relativistic information of stimulus, it cannot manipulate effect of previous choice on current decision, because it does not have previous choice variable. Further, lack of previous choice information in BFW result in it also cannot implement feedback information, because feedback was not assigned to previous stimulus but to response. However, both choice and feedback had a crucial role on the other studies (Mori & Ward, 1995; Lau & Glimcher, 2005; Stewart et al., 2005; Donkin et al. 2014). Also, BFW cannot generate assimilation effect, in which current choice has positive correlation with previous response, because criterion has no choice but to be attracted by previous stimulus. Because feedback and assimilation

effect are related with each other (Holland & Lockhead, 1968; Mattews & Stewart 2009), it looks very necessary for BFW to combine feedback effect to be more comprehensive model.

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국문 초록

베이시언 추론과 작동 기억에 기반한 지각 판단 기준 갱신 모델: 인간 행동과 뇌영상의 시행 간 변이에 대한 연구

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우리가 가진 입장은 주변 환경의 영향으로 바뀌곤 한다. 우리의 입장이 바뀌므로 판단을 하려는 대상이 같더라도 시간과 장소에 따라 그에 대한 판단의 결과는 일관적이지 않게 된다. 본 연구는 이렇게 인간의 의사 결정이 환경의 영향을 받아 달라지는 현상을 체계적으로 규명하기 위한 연구이다. 우리의 질문은 왜 그리고 어떻게 인간의 판단 기준이 때때로 변화하는가? 이다. 링(ring)을 이용한 지각 판단 과제를 통해 우리는 피험자들이 동일한 자극이 주어지더라도 이전에 자신이 경험한 내용에 따라 체계적으로 다른 판단을 내리는 현상을 통제된 실험 상황에서 재현할 수 있었다. 이 현상의 기저 원리를 이해하기 위해 작동 기억과 베이시언 추론을 이용한 의사 결정 모델과 그 모델의 단순화된 3개의 또 다른 모델들을 설계하였다. 이 모델들을 인간 행동과 뇌영상 데이터에 적용함을 통해서 우리는 피험자들이 동일한 자극에 대해 상이한 판단을 내리는 현상이 몇 초 이전에 경험한 여러 사물들의 정보에 영향을 받을 뿐 아니라 오랜 시간 변하지 않는 일반적인 사물의 크기에 대한 정보에 의해서도 영향을 받고 있다고 가정할 때에야 비로소 잘 설명된다는 것을 확인하였다. 아울러 각각이 장기, 단기 기억에 의존하는 그 상이한 두 정보는 베이시언 추론의 틀 안에서 하나의 정보로 통합 되어 과거에 사용했던 판단 기준을 미래에 사용될 기준으로 업데이트 시킬 수 있었다.

이러한 일련의 결과들을 놓고 우리는 인간의 세계에 대한 관점이 시시각각 변하는 이유는, 인간은 매 순간 의도하든 하지 않든, 최근에 경험한 새로운 정보와 기존에 고수하고 있던 입장을 모두 이용하여 매 순간 어떤 관점에 대해 가장 적절한 입장을 확률적으로 추론하고 있기 때문이라는 것을 제안하는 바이다.

Keywords : **지각 판단 결정, 판단 기준, 베이시언 추론, 기능성 자기 공명 영상, 각각 시도의 가변성, 판단 불확실성**
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